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BARYLAUS, NEW GENUS (COLEOPTERA: CARABIDAE) ENDEMIC TO THE WEST INDIES WITH OLD WORLD AFFINITIES

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Abstract.—The genus *Barylaus* is proposed for 2 endemic West Indian species of Carabidae; *Colpodes estriatus* Darlington (type species) from Puerto Rico, and *Colpodes puncticeps* Darlington from the Dominican Republic. The genus is described, and diagnoses and distributions of the species are presented. *Barylaus* is placed in the subtribe Caelostomina (tribe Pterostichini), based on synapomorphies shared with the genera *Mallopelmus* Alluaud, *Caelostomus* MacLeay, and *Hemitelestus* Alluaud. *Cyrtolaus* Bates is also transferred to the Caelostomina, making the subtribe pantropical. Based on an amphi-Atlantic vicariance hypothesis, the origin of the Caelostomina is estimated at 75–100 million years ago. A cladistic analysis is presented which supports the new subtribal limits. Recognition of the Caelostomina in the new sense results in the recognition of Pterostichini and Platynini as sister taxa.

In 1939, Philip Darlington wrote of a species of carabid beetle he had collected in the Dominican Republic:

> "This species is, in fact, completely isolated from all the species of Colpodes previously known to me, and I shall probably make it the type of a new genus in my final revision of the West Indian Carabidae" (p. 95).

Detailed examination of the mouthparts and internal reproductive structures of this and a related species from Puerto Rico indicates the need to propose a new genus in the tribe Pterostichini, subtribe Caelostomina Straneo (1942). In this paper, I describe the genus, and provide a key and diagnoses to the two known species. A cladistic analysis is presented which summarizes the derived character states of *Barylaus* shared with the Central American *Cyrtolaus* Bates, and exemplars of several Old World genera of the Caelostomina. Comparison of exemplar caelostomine taxa with the ground plans of the tribes Pterostichini and Platynini supports the recognition of these two taxa as sister taxa. Caelostomina in the new sense is expanded to include the endemic Neotropical genera *Barylaus* and *Cyrtolaus,* making the subtribe pantropical. A vicariance hypothesis provides an estimate of the age of the Caelostomina.

MATERIALS AND METHODS

Materials. Museum specimens were obtained with the assistance of the following curators, institutions, and individual collectors: George E. Ball and Danny Shpeley, University of Alberta (UASM); Ross T. Bell, University of Vermont (UV); Alfred F. Newton, Jr., Museum of Comparative Zoology, Harvard University (MCZ); Cornell University Insect Collection (CUIC); Julio Micheli, Ponce, Puerto Rico (JMi).

Methods. Whole specimens were examined using 8–100×. Male genitalia were dissected after clearing in cold 10% KOH and placed in glycerin for observation. Female reproductive tracts were cleared in cold KOH, stained in a Chlorazol Black suspension in methyl cellosolve, placed on a temporary glycerin slide with cover slip and examined using a dissecting microscope at low power, and a phase-contrast compound microscope at 100–200×.

The cladistic analysis was performed by hand using the Camin-Sokal algorithm (Sneath and Sokal, 1973) with the resultant procladogram modified to minimize steps. Transformation series polarities were determined by comparison of exemplar taxa with a wide range of out- and in-group taxa (Appendix I). A current classification of Carabidae (Erwin and Sims, 1984) permits estimation of likely out-groups, facilitating estimation of the primitive state of the characters (Watrous and Wheeler, 1981). For several exemplar taxa (Pterostichini, Platynini, *Cyrtolaus*) there are many possible generic or specific level taxa that could have been included. The tribes Pterostichini and Platynini are represented by what is considered the ground plan (Wagner, 1980) of each group. The ground plan is the minimal set of derived character states necessary to diagnose the group. The primitive character states for *Cyrtolaus* are taken from Whitehead and Ball (1975), or inferred from dissections of *Cyrtolaus subiridescens* Whitehead and Ball, and *C. ricardo* Whitehead and Ball.

Barylaus, new genus

Diagnosis. Compact shiny beetles with inflated convex elytra, cordate convex pronotum (Fig. 1), distinguishable from other Pterostichini by the following diagnostic characters: 1) elongate mouthparts; 2) frons and vertex with irregularly spaced pits; 3) pronotum without setae; 4) basal setigerous seta of elytron near base of 2nd interneur; 5) mesosternum with invaginated post-like apodeme (Fig. 8), evidenced externally by pit in mesosternum between fore-margins of mesocoxae; 6) elytra fused, metathoracic flight apparatus greatly reduced; 7) a series of large pits along lateral margins of elytra; 8) elytral plica developed internally, not visible externally as crossed elytral margin; 9) male copulatory organ inverted from typical pterostichine position, everted dextro-ventrally; 10) overall body length 4.0–7.0 mm.

Description. Body rotund, convex, head deflexed adding to round appearance. Body surface smooth, with reduced pronotal and elytral setation. Head elongate; frons with irregularly spaced pits; frontal furrows deep, clypeus somewhat inflated, separated from frons by impressed suture; labrum with 6 apical setae. Mandibles elongate (Figs. 2–5); right mandible bearing anterior, median, and posterior retinacular teeth (Fig. 3); both mandibles bearing 2 small dorsal pits. Maxilla with elongate lacinia, galea and palp (Fig. 6); lacinia with 2 peg-like setae accompanying thinner brush-like setae on internal margin; galea biarticulate, basal segment twice length of apical; palp with antepenultimate segment curved, thicker at middle, apical segment longer than penultimate. Labium (Fig. 7) with bisetose ligula; paraglossae membranous; palps 3-segmented, $3 > 2 > 1$ in length, apical segment inflated, palpiger nearly as long as 2nd segment. Mentum bisetose with well-developed pits. Antennae relatively short; scape with single apical seta, pedicel glabrous, antennomere 3 glabrous except for apical ring of setae, apical half of antennomere 4 and antennomeres 5–11 with fine dense setae.

Pronotum smooth, convex, cordate; lateral margins sinuate before nearly right or slightly acute, denticulate hind angles; median impression well developed, especially basally; latero-basal impressions smooth; basal bead absent; lateral setae absent; anterior transverse impression barely visible. Prosternal process broad, not margined, a broad median depression extending from between procoxae to near apical ⅓ of prosternum; sternum and episternum impunctate.

Elytra convex, fused, interneurs slightly impressed to not visible; scutellar interneur absent, basal elytral seta between 1st and 2nd interneur present; setae absent on elytral disc; a series of 5 or 9–10 pits situated along lateral margin of each elytron, the series of umbilicate lateral setigerous punctures interrupted by these foveae; lateral depression of elytron ending anteriorly at humerus; elytral plica developed internally (Fig. 15). Mesosternum somewhat pedunculate anteriorly; pit visible between anterior edges of mesocoxae which is due to large post-like apodeme (Fig. 8) which extends upward beneath the mesoscutellum. Metathorax short, metepisternum broader than long.

Legs relatively short. Pro- and mesocoxae with ventral condyle forming the ball of a ball and socket articulation. Femora moderately robust; tarsi not elongate, apical tarsomere with 2 pairs of ventral setae.

Abdomen heavily sclerotized; 1st and 2nd visible segments (segments II and III) fused laterally, segments III and IV fused medially; 3rd to 5th sutures with well-developed internal sulcus medially; apical sternite of females with 4 apical setae, males with 2 apical setae.

Male genitalia inverted from condition observed in noncaelostomine Pterostichini, the aedeagus everted to the right and then ventrally, lying in repose on the left side; parameres conchoid, glabrous, right paramere larger than left (Fig. 10). Female reproductive tract (only *B. estriatus* dissected) with biarticulate gonocoxae, the apical gonocoxite bearing 2 lateral and 1 dorsal setae (Fig. 13); basal gonocoxite bearing apical fringe of 4 to 7 setae. Spermathecal receptaculum with broad base joined to median oviduct near junction with bursa copulatrix, receptaculum base with fringe of ectodermal projections on hemocoelic surface; spermathecal gland duct entering near base of receptaculum.

Type species. Colpodes estriatus Darlington, described from El Yunque, Puerto Rico.

Generic name. Bary (heavy) + la-us (stone) alludes to the body shape of these beetles. The formation of the name emphasizes the affinities of *Cyrtolaus* Bates and *Barylaus.*

KEY TO THE ADULTS OF *Barylaus*

1. Elytral interneurs not visible, upper body smooth (Fig. 1); one seta over each eye; lateral margin of elytra with 5 large foveae; Puerto Rico .... *Barylaus estriatus*

1′. Elytral interneurs visible as linear impunctate impressions, elytral intervals broadly convex; no setae over eyes; lateral margins of elytra with 9–10 large foveae; Hispaniola .... *Barylaus puncticeps*

Barylaus estriatus (Darlington), **New Combination**

Colpodes estriatus Darlington, 1939, Mem. Soc. Cubana Hist. Nat. 13:96.

Diagnosis. In addition to key characters, distinguished from *B. puncticeps* by eyes of normal size, over 20 facets across diameter; aedeagus of male with median lobe

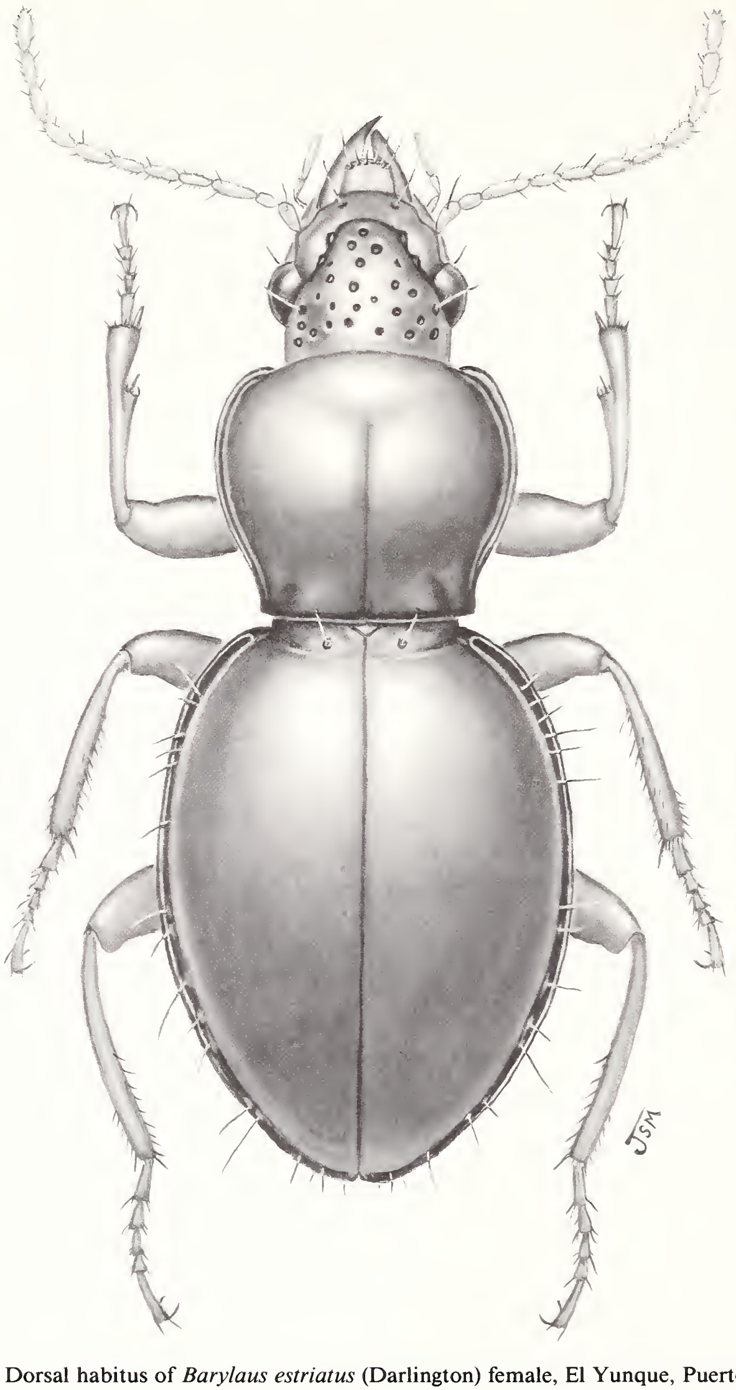
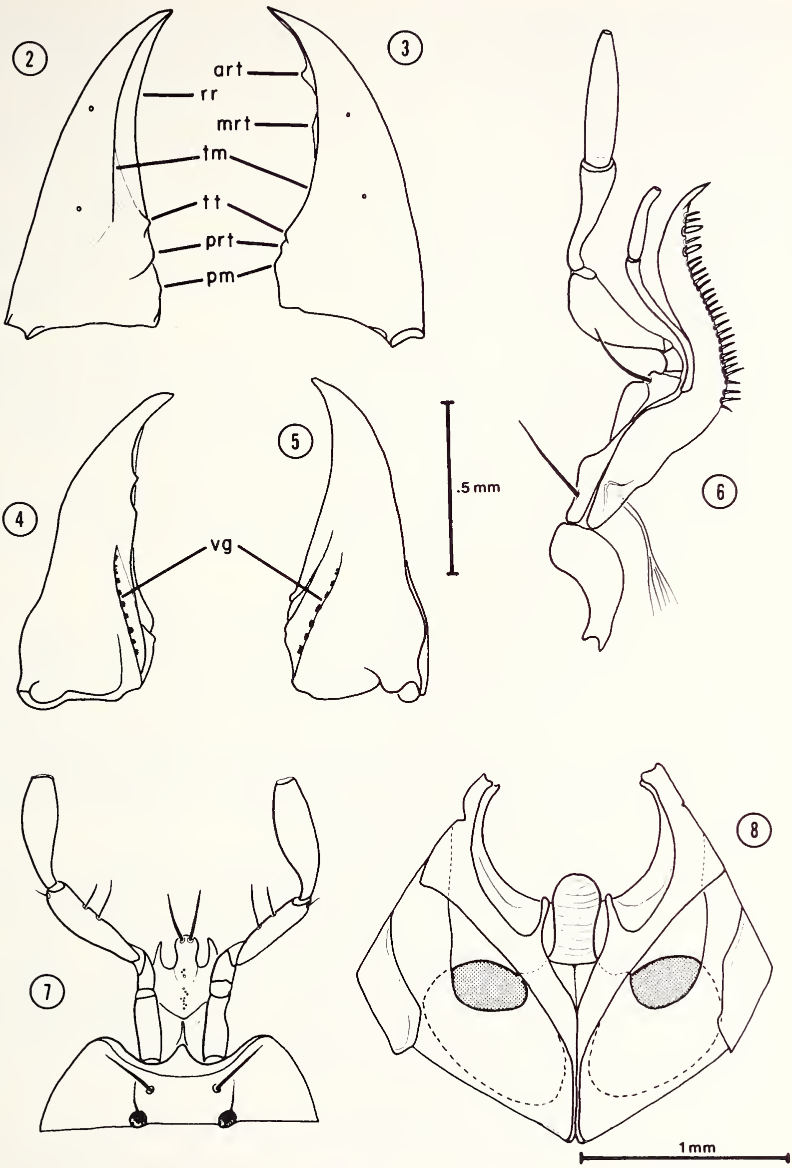


Fig. 1. Dorsal habitus of *Barylaus estriatus* (Darlington) female, El Yunque, Puerto Rico.



Figs. 2–8. 2–7. Mouthparts of *B. estriatus.* 2. Dorsal view of left mandible. 3. Dorsal view of right mandible. 4. Ventral view of right mandible. 5. Ventral view of left mandible. 6. Ventral view of right maxilla. 7. Ventral view of labium and mentum. (Scale bar is 0.5 mm; art = anterior retinacular tooth; mrt = median retinacular tooth; prt = posterior retinacular tooth; rr = retinacular ridge; tm = terebral margin; pm = premola; vg = ventral groove.) 8. Ental view from posterior of meta- and mesosternum, showing mesosternal post between mesocoxae. (Openings of coxal socket stippled; scale bar 1 mm.)

evenly curved (Fig. 9), small denticles near apex; internal sac of median lobe with basal band of sclerotized teeth and apical field of spicules surrounding gonopore.

Distribution records. PUERTO RICO: El Yunque, 3,000 ft elev., May 1938, Darlington (type series, 32 specimens); 3,000–3,300 ft elev., Feb 15–24, 1969, T. and B. Hlavac and L. Herman (3, MCZ); Jan 2, 1970, R. and J. Bell (3, UV); Caribbean Nat. For., Mte. Britton, 950 m elev., May 10, 1985 (3, CUIC), May 13, 1985 (10, CUIC), S. W. Nichols, E. R. Hoebeke, and J. K. Liebherr; Toro Negro For., Vereda el Bolo, 675 m elev., May 7, 1985, E. R. Hoebeke and J. K. Liebherr (3, CUIC); Guilarte For., April 20, 1975, J. Micheli, swept from foliage (1, JMi); Mte. Guilarte, base of summit trail, 925 m elev., May 5, 1985, S. W. Nichols, E. R. Hoebeke, and J. K. Liebherr (5, CUIC); Maricao For., 2,000–3,000 ft elev., Jun 2, 1938, Darlington (1, MCZ).

Biology and habits. Darlington (1939) reported *B. estriatus* running on rotten logs at night. All of the specimens collected in 1985 were associated with rotten logs or rotten palm fronds. Beetles were found on the underside of logs or fronds, often clinging upside down to the surface. Beetles were not found on the very wet to saturated soil surface.

The beetles exhibit a well-developed defensive posture when disturbed, in which they lie motionless with legs and antennae tucked against the body. This posture may be held for as long as 20 to 30 seconds.

Barylaus puncticeps (Darlington), **New Combination**

Colpodes puncticeps Darlington, 1939, Mem. Soc. Cubana Hist. Nat. 13:94.
Colpodes puncticeps compactus Darlington, 1939, *ibid.*:95.

Diagnosis. Key characters can be augmented by the following to diagnose *B. puncticeps*: eye reduced in size, approximately 9 facets across diameter; aedeagal median lobe of male with internal (ventral) margin swollen (Fig. 11), internal sac without sclerotized basal band of teeth or apical spicules.

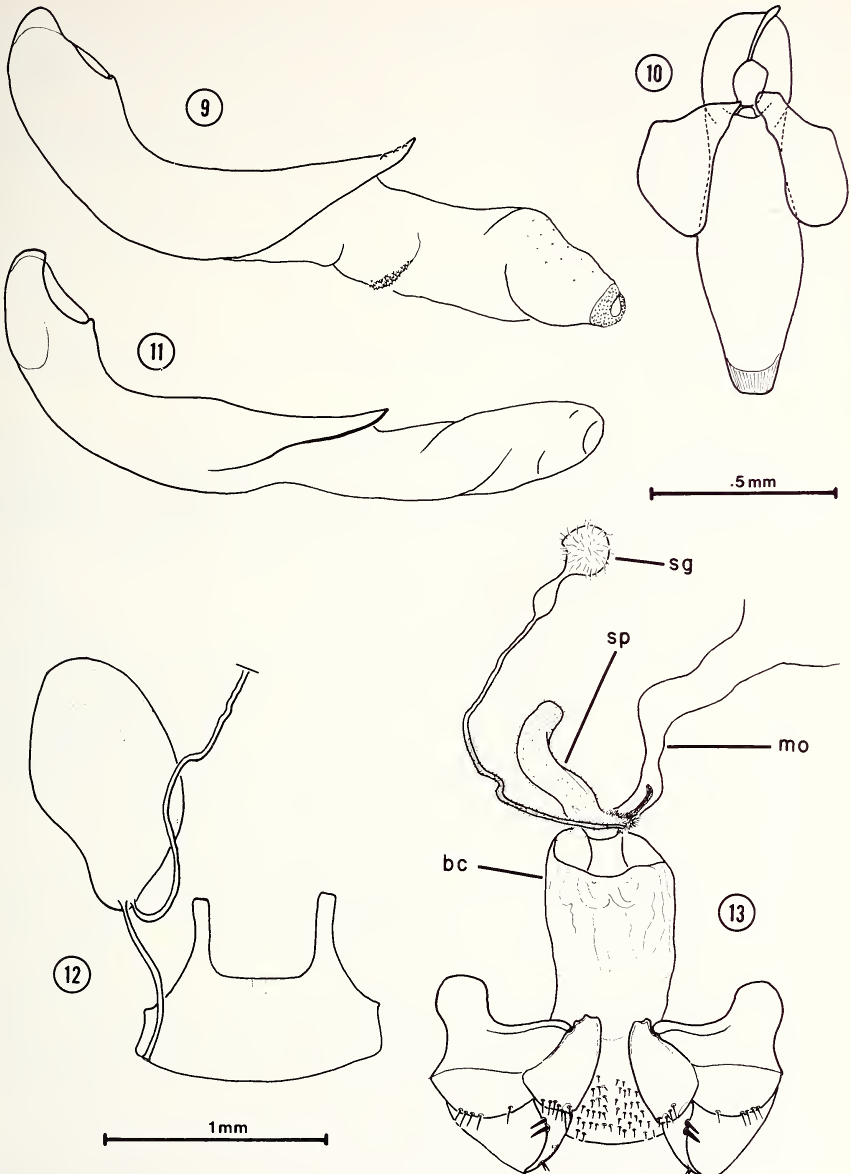
There are 6 known specimens of this species, of which I have seen 4: a male and female of each subspecies. Darlington (1939) lists differences in body part ratios which discriminate the two subspecies. Whether these differences represent geographic variation or inadequate sampling must await additional material.

Distribution records. B. p. puncticeps is known from DOMINICAN REPUBLIC: Loma Rucilla and mtns. N, 5,000–8,000 ft elev., June 1938, Darlington (type series, 3 specimens). *B. p. compactus* is known from D.R.: cloud forest vic. Valle Nuevo, ca. 6,000 ft elev., Aug 1938, Darlington (type series, 3 specimens).

PHYLOGENETIC AFFINITIES OF *Barylaus*

Straneo (1942) used the following characters to diagnose the pterostichine subtribe Caelostomina: 1) copulatory organ of male inverted; 2) umbilicate series on elytra interrupted toward the middle of their length; 3) setigerous pore at the base of the elytra positioned upon the third interval. Jeannel (1948) reports the Caelostomina as the only Old World Pterostichini (=subfamily Pterostichitae *sensu* Jeannel) possessing an inverted aedeagus.

Whitehead and Ball (1975) proposed the monogeneric subtribe Cyrtolaina to in-



Figs. 9–13. Median lobe of aedeagus of *B. estriatus,* dorso-lateral view. 10. Aedeagus of *B. estriatus,* ventral view. 11. Median lobe of *B. puncticeps,* dorso-lateral view. 12. Tergite 8 and defensive gland reservoir of *B. estriatus,* ventral view. 13. Female reproductive tract of *B. estriatus,* ventral view (bc = bursa copulatrix; mo = median oviduct; sg = spermathecal gland; sp = receptaculum of spermatheca). (Scale bar for 9–11, 13 is 0.5 mm; scale for 12 is 1 mm.)

Table 1. Character states for 12 characters and 7 taxa included in cladistic analysis (0 = primitive state; 1 = derived state).

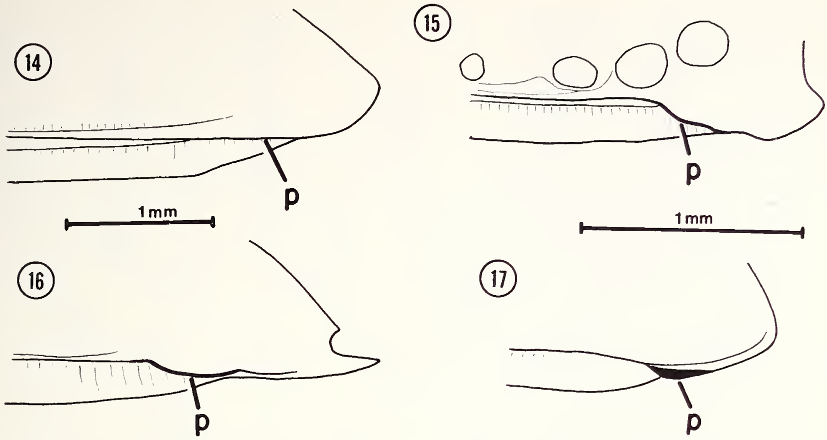
	Characters											
Taxon	1	2	3	4	5	6	7	8	9	10	11	12
Pterostichine ground plan	0	1	0	0	0	0	0	0	0	1	0	0
Cyrtolaus	0	1	1	0	0	0	0	1	1	0	0	1
Barylaus	0	0	1	1	0	1	0	1	1	0	1	0
Mallopelmus	0	1	1	1	0	1	0	1	1	0	0	0
Hemitelestus	0	1	1	1	1	1	1	1	0	1	1	0
Caelostomus	0	1	1	1	1	1	1	1	0	1	1	0
Platynine ground plan	1	0	0	0	0	0	0	0	0	0	0	1

clude *Cyrtolaus* Bates. This genus also exhibits the inverted aedeagus, but in general is more platynine-like, with the majority of the species possessing elytra without an externally visible plica. The Cyrtolaina were proposed as a subtribe that bridged the gap between the pterostichine and platynine lines, which in Whitehead and Ball's opinion necessitated inclusion of the Platynini within the Pterostichini.

To illustrate the phylogenetic relationships of *Barylaus* and these taxa, a cladistic analysis is presented which is based on the following taxa: 1) 3 taxa assigned by Straneo to the Caelostomina (*Mallopelmus* [*Trichillinus*] *linearis* Alluaud, *Hemitelestus hova* Alluaud, *Caelostomus picipes* MacLeay); 2) *Barylaus estriatus*; 3) *Cyrtolaus* spp.; 4) pterostichine ground plan; 5) platynine ground plan. The pterostichine and platynine ground plans are inferred from out-group comparison (Appendix I). Characters included are restricted to those possessed in derived state in 2 or more of the taxa. The characters and the rationale for assignment of character states are presented below. Character states of the taxa are summarized in Table 1.

Characters 1, 2. The elytral plica can be variously developed. In *Cicindela, Carabus, Nebria,* and *Blethisa* it is absent. Platynini and Harpalini also lack a plica, or any evidence of a lock mechanism on the internal surface of the elytra (Fig. 14). But, many taxa in the Carabinae possess an internal ridge that locks the abdomen and elytra (e.g., *Omophron, Loricera, Pasimachus, Patrobus, Diplous, Psydrus*). Thus at the level of the Pterostichini and Platynini the presence of an internally developed plica is considered primitive (Figs. 15, 16). Specialization is judged to have proceeded in 2 directions; 1) toward total absence of the plica internally or externally (states 1, 0; Fig. 14); 2) toward a fully developed externally visible plica as seen in most Pterostichini (states 0, 1; Fig. 17).

Character 3. The carabid lacinia generally bears fine brush-like setae on the inner margin of equal thickness throughout its length (state 0). In *Cyrtolaus, Barylaus, Mallopelmus, Hemitelestus,* and *Caelostomus,* there are 2 to 5 thicker peg-like setae on this margin near the lacinial tip in addition to the finer brush-like setae basally (Fig. 6; state 1). Straneo (1942) reports such setae from most Caelostomina, *Cosmodiscus* Sloane, and several other genera. Thicker setae are regularly spaced between fine setae along the lacinial margin in *Platynus veracrucensis* (Barr), a species with elongate mouthparts. But the thicker setae in *P. veracrucensis* are not as thick or



Figs. 14–17. Internal view of right elytral tip, showing internal development of plica (p). 14. *Platynus cychrinus* (Darl.). 15. *Barylaus estriatus* (Darl.) (circles above plica represent inner surface of elytal foveae). 16. *Cyrtolaus ricardo* Whd. and Ball. 17. *Caelostomus picipes* MacL. (Scale bar for 14, 16 on left, for 15, 17 on right.)

blunt relative to the fine setae as observed in *Barylaus*. Peg-like setae on the lacinia are also observed in *Ardistomis* (S. W. Nichols, pers. comm.), a genus characterized by elongate mouthparts. Such specialization of lacinial setae may be associated with elongation of mouthparts.

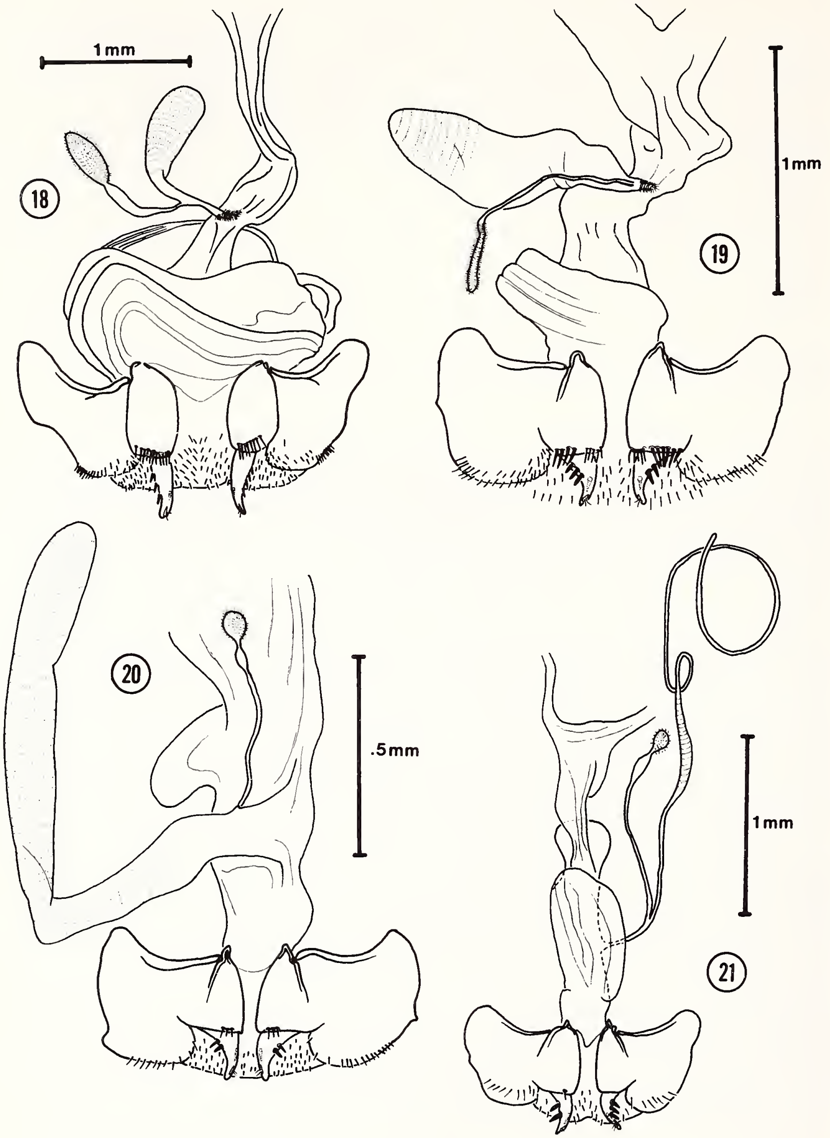
Characters 4, 5. The basal elytral seta is situated at the juncture of the interneurs 1 and 2 in most Carabidae (states 0, 0). With the fusion of the scutellar interneur to the base of the sutural interneur, this seta appears to be at the base of the 2nd interneur in *Barylaus* and *Mallopelmus* (states 1, 0). *Caelostomus* and *Hemitelestus* have this seta at the base of the 3rd interneur (states 1, 1).

Character 6. Dorsal elytral setae are observed throughout the Carabidae (state 0), whereas *Barylaus, Mallopelmus, Hemitelestus,* and *Caelostomus* possess no dorsal setae (state 1).

Character 7. Carabidae generally possess umbilicate elytral punctures on the apical half of the elytral margin that are not separated into distinct groups (state 0). *Caelostomus* and *Hemitelestus* have these setae positioned in 2 groups with a large intervening space without setae (state 1).

Character 8. Cyrtolaus, Barylaus, and the 3 Old World genera of Caelostomina have the aedeagus inverted (state 1) from the typical position seen in most Harpalinae. Reversal of the aedeagus is also observed in *Pristosia* Motschulsky (Lindroth, 1956) and *Calathus ovipennis* Putzeys (Ball and Negre, 1972), of the platynine subtribe Sphodrina. The derived nature of the styloid parameres in *Pristosia* and *C. ovipennis,* plus other characters, unite them with other Sphodrina, indicating that reversal of aedeagal position is a parallel derivation in these taxa.

Character 9. The setose-like patch of ectodermal filaments on the base of the spermatheca where it joins the median oviduct (state 1; Figs. 13, 18, 19) is known



Figs. 18–21. Female reproductive tracts, ventral view (scale bars with figures). 18. *Cyrtolaus ricardo* Whd. and Ball. 19. *Mallopelmus linearis* All. 20. *Caelostomus picipes* MacL. 21. *Hemitelestus hova* All.

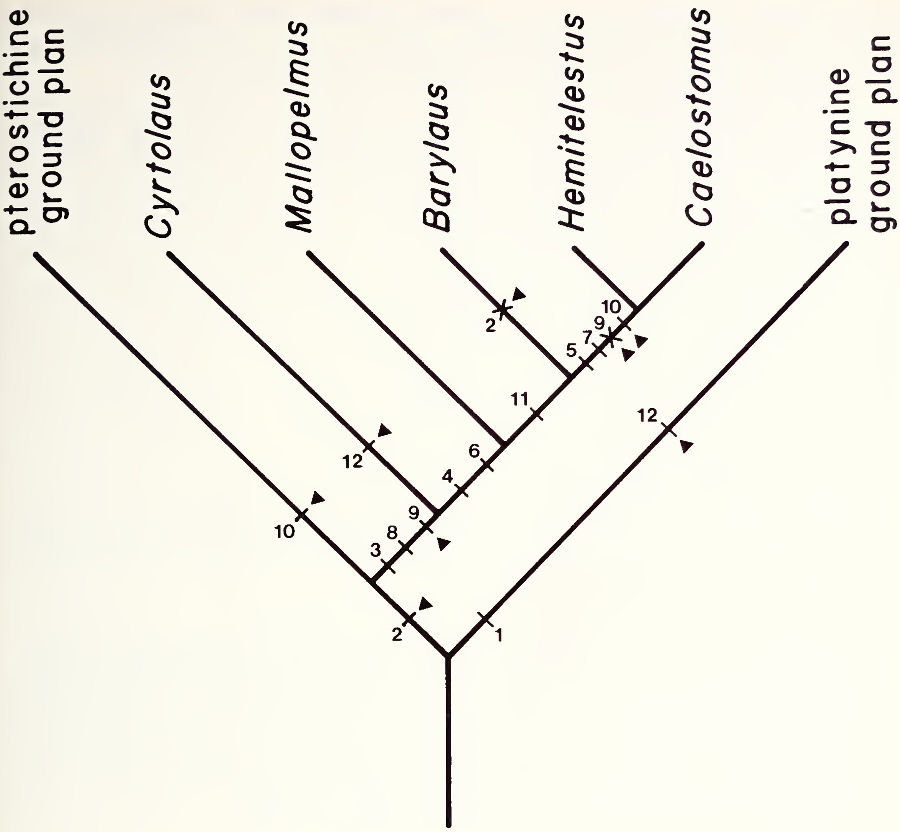


Fig. 22. Cladogram showing relationships of caelostomine genera to pterostichine and platynine ground plans (characters that change state more than once on cladogram have triangular flags; state gains shown by slashes, reversals to primitive state by x's).

only from *Cyrtolaus, Barylaus,* and *Mallopelmus. Cyclotrachelus sodalis* LeConte possesses a similar fringe with broader filaments, but this is assumed an independent derivation.

Character 10. The basal gonocoxite bears a fringe of setae in many Platynini and various carabid genera (e.g., *Carabus, Nebria, Blethisa, Thalassotrechus, Trechus, Patrobus, Amara,* and *Harpalus*). Glabrous or nearly glabrous basal gonocoxites are present in many Pterostichini and in *Caelostomus* and *Hemitelestus* (Figs. 20, 21). Reduction of the setal fringe is considered derived.

Character 11. The hemisternites of the 9th segment commonly bear many setae in more than one row (Figs. 18, 19). These setae are reduced to a single row in *Barylaus, Caelostomus,* and *Hemitelestus* (state 1; Figs. 13, 20, 21).

Character 12. The Platynini possess a well-developed dorsal lobe on the defensive gland reservoirs (state 1), a condition similar to that seen in the somewhat closely related Anthiini (Forsyth, 1972). Variously developed dorsal lobes are present in different tribes of the Harpalinae. *Cyrtolaus* also possesses such a lobe. The pterostichine defensive gland lacks the lobe, as in *Barylaus* (state 0; Fig. 12).

The most parsimonious cladogram places *Cyrtolaus, Mallopelmus, Barylaus, Hemitelestus,* and *Caelostomus* in one monophyletic group more closely related to the pterostichine ground plan than to the platynine ground plan (Fig. 22). There are 16 steps on the cladogram, with 4 characters changing state more than once. The development of an externally visible elytral plica is the only means of diagnosing Pterostichini. The loss of an internal elytral lock appears a derivation of the Platynini. In this analysis, *Cyrtolaus* is assumed to possess an elytral plica in fully developed condition, even though the more derived species within the genus have it in partially developed state (Fig. 16; Whitehead and Ball, 1975). Based on the most parsimonious cladogram, *Barylaus* has similarly lost a fully developed plica. The possession of an internal elytral plica in these taxa is considered a parallel secondary development. Other similarities of *Cyrtolaus* spp. and *Barylaus* include fused elytra, and very heavily sclerotized abdominal sclerites. With such developments, an internal elytral plica may suffice to strongly lock abdomen and elytra.

On the cladogram the derived character states of inverted aedeagus and lacinial peg-like setae unite *Cyrtolaus, Mallopelmus, Barylaus, Hemitelestus,* and *Caelostomus.* Based on these characters, plus the fringe on the base of spermatheca (character 9) and elytral setation (characters 4, 6), *Barylaus* is considered a member of the subtribe Caelostomina. A comprehensive study including all caelostomine genera is desirable, but the synapomorphies presented here strongly support such placement. *Cyrtolaus* is likewise best placed in the Caelostomina, although it possesses more primitive characters shared with the Platynini. The presence of a dorsal lobe on the defensive gland reservoirs in *Cyrtolaus* (character 12) does not support this placement. The occurrence of variously developed dorsal lobes in different lineages of the Harpalinae suggests parallel derivation of this character.

CONSEQUENCES OF CAELOSTOMINA IN THE NEW SENSE

The recognition of *Cyrtolaus* and *Barylaus* as New World representatives of the Caelostomina has several consequences. First, the Pterostichini and Platynini are best treated as sister taxa of tribal rank. The Pterostichini possess a well-developed externally visible elytral plica, which has apparently been reduced in several lineages. The Platynini is the more generalized taxon, which may also have spawned various lebiomorph lineages.

Secondly, if the statement of caelostomine relationships in Figure 22 is overlaid on the geographic distribution of the taxa included in the analysis (Fig. 23), an hypothesis of amphi-Atlantic vicariance can be proposed to account for the phylogenetic relationships. Both *Cyrtolaus* and *Barylaus* contain wingless upland species with very reduced metathoraces. This specialization occurs repeatedly in Carabidae, and based on the presence of wings in *Mallopelmus, Hemitelestus,* and *Caelostomus,* has occurred independently in *Cyrtolaus* and *Barylaus.* Nonetheless, amphi-Atlantic vicariance is a reasonable hypothesis. If it did occur, it would date the origin of the Caelostomina at late Cretaceous, 75–100 million years ago, when South America and Africa completed their separation (Smith et al., 1973; Anderson and Schmidt,

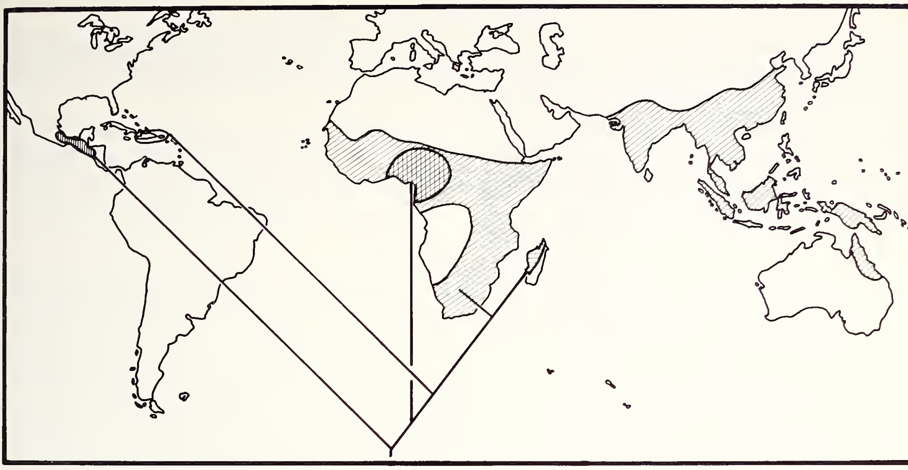


Fig. 23. Area-cladogram of 5 exemplar Caelostomine taxa: *Cyrtolaus* (dense vertical hatching); *Mallopelmus* (*Trichillinus*) (wide vertical hatching); *Barylaus* (open); *Hemitelestus* (horizontal hatching); *Caelostomus* (diagonal hatching).

1983). The great age of the Caelostomina is supported by the distribution of the 2 subgenera of *Mallopelmus*; sg. *Trichillinus* Straneo distributed in West Africa, and *Mallopelmus s. str.* restricted to Madagascar (Straneo, 1942). Madagascar reportedly rifted from the Kenya-Somalia coast at least 90 million years ago (Rabinowitz et al., 1983), a time estimate supporting an hypothesis of Cretaceous vicariance in this genus. The age of divergence for the Pterostichini and Platynini would predate the estimate for age of the Caelostomina.

Barylaus is more closely related to Old World taxa than it is to the Central American relict, *Cyrtolaus* (Figs. 22, 23). Such a result emphasizes the isolation of Puerto Rico and Hispaniola from Central America, especially when upland taxa are considered. It also emphasizes that geographic distribution should not color cladistic analysis.

Other insect groups in the West Indies exhibit African affinities. Brown (1978) summarizes butterfly distributions, concluding that several groups of long duration in the West Indies are as closely related to African as to Neotropical groups. Flint (1977) reports a small African influence in the West Indian faunas of Odonata and Trichoptera. The genus *Halocoryza* Alluaud (Carabidae: Scaritini) possesses an amphi-Atlantic distribution which includes the West Indies, but Whitehead (1966) attributes this distribution to past dispersal. *Caelostomus punctifrons* MacLeay, of West Africa, is introduced into Jamaica (Erwin and Sims, 1984). But, *Barylaus* and *Cyrtolaus* are poor candidates for long distance dispersal, as they both are comprised of upland flightless forest dwelling species of low population density. In specific, their biology, distribution, and phylogenetic relationships to Old World taxa strongly support an hypothesis of amphi-Atlantic vicariance. In general, they illustrate that Africa cannot be ignored when searching for nearest relatives of West Indian and Central American endemics.

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APPENDIX I

List of taxa used to polarize character transformation series and determine pterostichine and platynine ground plans.

Cicindela longilabris Say
Carabus nemoralis Mueller
Omophron dentatum LeConte
Nebria eschscholtzi Ménétriés
Blethisa multipunctata L.
Loricera foveata LeConte
Pasimachus elongatus LeConte
Bembidion planatum LeConte
Thalassotrechus barbarae Horn
Trechus chalybeus Dejean
Psydrus piceus LeConte
Patrobus longicornis Say
Diplous californicus Motschulsky
Synuchus impunctatus Say
Platynus cincticollis Say
Platynus decentis Say
Platynus veracrucensis Barr
Anchomenus picticornis Newman
Rhadine caudata LeConte
Agonum extensicolle Say
Myas coracinus Say
Pterostichus angustus Dejean
Pterostichus haldemani LeConte
Pterostichus lucublandus Say
Pterostichus menetriesi Motschulsky
Pterostichus stygicus Say
Abacidus permundus Say
Cyclotrachelus sodalis LeConte
Amara blanchardi Hayward
Harpalus erraticus Say
Anisodactylus discoideus Dejean